A revision of the fossil taxa assigned to *Hyperaulax* (Gastropoda: Odontostomidae), with the description of a new genus (Gastropoda: Bulimulidae)

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ABSTRACT

Orthalicoid terrestrial snails recorded from the lower Miocene portion of the upper Oligocene to lower Miocene Tampa Member of the Arcadia Formation (Hawthorn Group) of southern Florida and the lower Miocene St. Marks Formation of northern Florida are reviewed. These taxa, previously allocated to the genus *Hyperaulax* Pilsbry, 1897 (Odontostomidae), are reassigned to *Tocobaga* new genus (Bulimulidae) on the basis of a distinctive suite of morphological characters, particularly those of the peristome and the embryonic whorl sculpture. Examination of all type material of the fossil taxa historically assigned to *Hyperaulax* reveals that only three species are separable (*Partula americana* Heilprin, 1886; *Bulimulus americanus wakullae* Mansfield, 1937; and *Bulimus floridanus* Conrad, 1846). The varietal names *Bulimulus americanus* var. *partulinus* and *B. americanus* var. *laxus*, both Dall, 1890, are indistinguishable from the nominate form in any important morphological character. *Bulimulus heilprinianus*, *Bulimulus stearnsii*, both Dall, 1890, and *Bulimulus ballistae*, *Bulimulus remolina*, *Bulimulus tampae*, and *Bulimulus tortilla*, all Dall, 1915, are synonyms of *B. floridanus* Conrad, 1846. The status of *B. a. wakullae* from northern Florida is problematic. Although clearly not conspecific with *P. americana*, it is tentatively assigned to *Tocobaga* new genus and is herein elevated to species level. The biogeography of *Tocobaga* new genus is tentatively discussed. Fossiliferous deposits in North America and South America have not yielded taxa with the combination of shell characters found in the new genus and relationships with other bulimulid genera are unknown. However, it is probable that the new genus, like other non-marine mollusks from the Tampa Member of the Arcadia Formation, dispersed to Florida after contact between the Caribbean Plate and the Bahama Platform (circa 38 Ma).

Additional Keywords: Tocobaga new genus, Miocene, Florida

INTRODUCTION

Hyperaulax Pilsbry, 1897a (type species, *Bulimulus ridleyi* E. A. Smith, 1890) was described as a subgenus of *Bulimulus* Leach, 1814 (Bulimulidae Tryon, 1867) to encompass taxa having axial wrinkles on the embryonic whorls and a distinct channel at the posterior insertion of the outer lip. Pilsbry (1901: 102–103) elevated *Hyperaulax* to genus level with the "section" *Bonnanius* Jousseaume, 1900 and transferred it to the then subfamily Odontostominae, but did not alter the composition of the taxon, which consisted of the extant *H. ridleyi* and *H. ramagei* (both E.A. Smith, 1890) from Fernando Noronha Island, Brazil and several upper Tampa Member (Arcadia Formation) species from the Ballast Point site in Florida. Another fossil species from the western United States, *Bulimulus limnaeiformis* Meek and Hayden, 1856 was tentatively transferred to *Hyperaulax* by Wenz (1923: 731), but is now assigned to the Viviparidae (see Henderson, 1935 for references). *Bonnanius* Jousseaume, 1900 is currently treated as a distinct genus (Simone, 2006; Breure and Ablett, 2012), type species *B. ramagei*, thus restricting *Hyperaulax* to its type species *H. ridleyi* and the Florida fossil species. The basis for the assignment of the fossil species to *Hyperaulax* was the striking similarity in shell shape, size, and peristome characters between the fossil taxa and the extant *H. ridleyi* and, in particular, the presence in all taxa of a narrow channel at the junction of the outer lip with the body whorl (Pilsbry, 1897b: 82; 1901: 102–103).

Recently, we examined numerous specimens of Ballast Point bulimulids housed in the Invertebrate Paleontology Collection at the Florida Museum of Natural History (FLMNH) and all type material of Florida fossil taxa assigned to *Hyperaulax*. We concluded that several unnecessary names had been introduced for the Florida fossils. By comparing these fossil specimens to *Hyperaulax ridleyi* and the type species of all other pertinent bulimulid genera and subgenera, we find that the placement of the

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early Miocene fossils is best resolved by formally recognizing their distinctive suite of characters with a new generic epithet. We therefore adopt the name:

SYSTEMATIC PALEONTOLOGY

Tocobaga new genus

Diagnosis: Shell ovate to ovate-cylindrical in shape. Whorls 5.5–6; embryonic whorls approximately 1.2 –1.3, bluntly rounded and spirally striate; later whorls sculptured with weak to moderately strong axial riblets, spiral incised lines often present in interspaces, occasionally crossing axial riblets; last half of body whorl slightly flattened behind peristome, ascending for last 0.2 whorl; sutures shallow to well-impressed. Peristome broadly expanded and thickened internally, often strongly thickened basally; inner and outer margins connected by distinct parietal callus, interrupted by narrow channel at posterior insertion of outer lip; marginal palatal tooth robust, weak or lacking; when prominent, forming distinct sinus at upper insertion of outer lip, buttressed below. Aperture ovate to subquadrate in shape. Columella simple, lacking lamellae. Umbilicus narrow, chink-like.

Type Species: *Partula americana* Heilprin, 1886. Ballast Point, Hillsborough Bay, Hillsborough County, Florida, upper Tampa Member, Arcadia Formation (early Miocene).

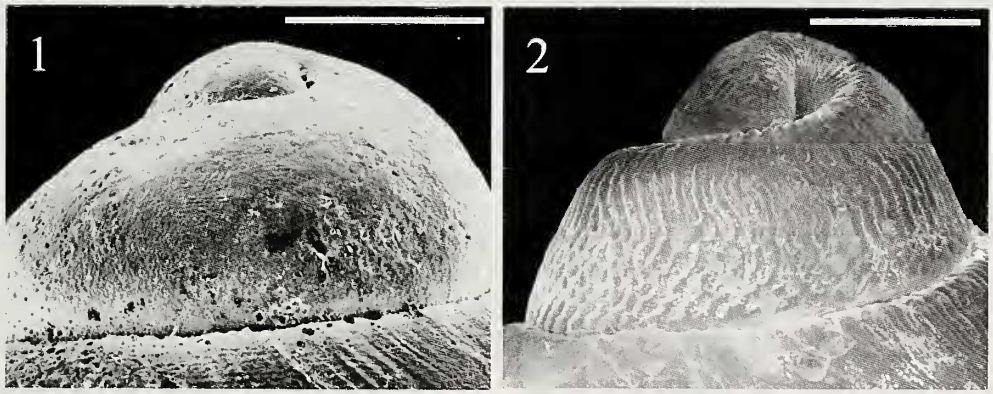
Content: *Tocobaga americanus* (Heilprin, 1886), *T. floridanus* (Conrad, 1846), and *T. wakullae* (Mansfield, 1937).

Etymology: The name *Tocobaga* is derived from the Tocobaga Tribe of Native Americans that, like these extinct snails, inhabited the Tampa Bay region, albeit 23 million years later. Tocobaga was first used in Spanish documents of the 1560s in reference to the male chief of the group, the chief's village, as well as the people themselves. Since no gender was implied when the name was established, we treat the genus name *Tocobaga* as masculine.

Discussion: The primary shell character used to differentiate many genera of Orthalicoidea Albers, 1860 is the embryonic whorl sculpture (Pilsbry, 1895, 1896). The efficacy of this character is supported at least in part by independent genetic evidence (Breure and Romero, 2012). The embryonic whorl sculpture of *Tocobaga americanus* is microscopically spirally striate (Figure 1) while that of *Hyperaulax ridleyi*, the type species of that genus, is axially wrinkled (Figure 2). This character alone serves to remove the fossil species from *Hyperaulax*. In addition, the first embryonic whorl of the Florida fossils is low, rounded with a weakly impressed suture (Figure 1), while that of *H. ridleyi* is greatly elevated, with a deeply channeled suture (Figure 2). These features of the embryonic whorl clearly indicate that the fossil taxa have been erroneously assigned to *Hyperaulax*.

The early assignment of these species to the orthalicoid family Bulimulidae was logical given their close resemblance in gross shell morphology to several extant bulimulid taxa and the biogeography of the Caribbean Basin. The only families outside the orthalicoids that serve as reasonable alternatives to this arrangement on the basis of shell morphology are the Partulidae and Enidae. In fact, Heilprin (1886) described *T. americanus* as a species of *Partula* Férussac, 1821, and Moellendorff (1901) suggested that *H. ridleyi* belonged to the enid genus *Napaeus* Albers, 1850. Hence, the evidence for the placement of the fossil taxa in the Bulimulidae is examined below.

The fossil species are readily distinguished from partulids by a variety of features. Of greatest importance are features of the embryonic whorls. Both partulids and *Tocobaga* have spirally striate embryonic whorls, but the striae of the partulids are much coarser. The embryonic whorls of partulids are conic and flat-sided, with barely any relief at the suture; the embryonic whorls of *Tocobaga* are rounded at the periphery, more globose, and with more distinct sutures. The later whorls of partulids are more rapidly expanding than those of *Tocobaga* and the



Figures 1–2. Embryonic whorl sculpture of *Tocobaga* new genus and *Hyperaulax*. **1.** *Tocobaga americanus* (Heilprin, 1886). UF 66651 (Invertebrate Paleontology Collection). **2.** *Hyperaulax ridleyi* (E.A. Smith, 1890). UF 109915 (Malacology Collection). Scale bar = 0.5 mm.

shells typically have an incomplete peristome lacking the parietal callus and associated groove at the junction of the outer lip with the body whorl that characterizes *Tocobaga*. From these characters it can readily be seen that the relationship of the early Miocene fossils is not with the partulids.

Separating *Tocobaga* from the Enidae on the basis of shell morphology is more difficult. Many enid taxa have shell morphologies very similar to that of *Tocobaga* (i.e., a channel at the posterior insertion of the outer lip and an expanded peristome). Enid embryonic whorls may be smooth or spirally striate. The fossil genus *Dendropupa* Owen, 1859 (see below), has axial sculpture on the embryonic whorls (Solem and Yochelson, 1979). The enid body whorl may ascend behind the peristome, but does not become flattened near the aperture as in *Tocobaga*. The primary reason for excluding *Tocobaga* from assignment in the Enidae is biogeographic. The enids are currently restricted to Europe, northern Africa, central and southern Asia, and the Pacific from Indonesia to Melanesia. Known fossils of this family are restricted to the same locations with the exception of *Dendropupa*, which has been collected from Upper Carboniferous sediments in eastern Canada, France, and Poland (Solem and Yochelson, 1979). Other enid fossils are known from the Paleocene of Europe and later records through the Tertiary of Europe, Africa, and the Middle East through Central Asia to China (Zilch, 1959). Solem and Yochelson's assignment indicates a possible Laurasian origin for the Enidae and a distribution of *Dendropupa* that pre-dates the separation of North America and Europe. However, the Enidae is unknown in subsequent North American land snail faunas and there is no other evidence that it constituted a component of the American Miocene fauna. Thus, we agree with Pilsbry (1901) that the resemblance of *Hyperaulax* and the Florida fossils to certain members of the Enidae is most likely the result of convergent adaptations to dry habitats. The thickened peristome allows for an efficient shell/substrate seal during aestivation, while the canal acts as a contact to the exterior.

The current geographic distribution of Orthalicoidea including the Bulimulidae strongly suggests that bulimulids could be expected in the fossil fauna of the Caribbean Basin, including early insular environments on the Florida Platform. Among Orthalicoidea families, *Tocobaga* is best assigned to the Bulimulidae. It is readily separated from the Amphibulimidae P. Fischer, 1873 (e.g., *Amphibulima* de Montfort, 1810) on the basis of shell shape and degree of calcification. The fossils do not belong with the Orthalicidae Albers, 1860 (e.g., *Liguus* de Montfort, 1810) because those taxa have larger, imperforate shells and a simple lip. *Tocobaga* cannot be assigned to the Odontostomidae because of the elevated embryonic whorls of the latter, lacking in spiral sculpture as discussed above. In addition, most odontostomids have apertural barriers. Hence, we agree with earlier authors that the Florida fossil species are properly assigned to the Bulimulidae.

The distinctively striate embryonic whorls of *Tocobaga* differ from all other North American and Antillean Bulimulidae which are either axially ribbed as in *Bulimulus* Leach, 1814 and *Rabdotus* Albers, 1850, or both axially and spirally ribbed as in *Drymaeus* Albers, 1850. Dall (1890) tentatively assigned all Florida taxa known at that time to the South American group *Anctus* Martens, 1860, based on similarities such as a laterally compressed body whorl behind a broadly reflected peristome. However, the embryonic whorls of *Anctus* are smooth and lack the channeled and calloused parietal area. Only the South American genera, *Lopesianus* Weyrauch, 1958, *Leiostracus* Albers, 1850, *Discoleus* Breure, 1978, and some *Bostryx* sensu lato Troschel, 1847 possess a similarly striate embryonic whorl sculpture. Of these genera, *Lopesianus* differs from *Tocobaga* in having fewer and stronger spiral striae on the embryonic whorls (Weyrauch, 1958: pl. 6, figs. 8); deeply channeled, crenulate sutures; no parietal callus; and an incomplete, simple peristome. *Leiostracus* differs in having the spiral striae confined to the lower half of each whorl; papilliform embryonic whorls; and an incomplete peristome only slightly expanded. *Discoleus* differs in having a larger, more bulbous embryonic whorl; a subovate aperture; more convex whorls; and a simple, incomplete peristome.

The polyphyletic genus *Bostryx* sensu lato (Breure and Romero, 2012) is the most difficult genus from which to distinguish *Tocobaga*, a reflection of the presumably diverse nature of the former. In each of several characters, one or a few species of *Bostryx* sensu lato can be found that approach the state seen in *Tocobaga*. However, in no case does any species of *Bostryx* sensu lato approach the entire suite of characters that serve to distinguish the fossils from other Bulimulidae.

We examined the type species of all but two (*Elatibostryx* Weyrauch, 1958 and *Kionoptyx* Haas, 1966) of the 21 generic synonyms (or subgenera) given by Breure (1979) as belonging to *Bostryx* sensu lato to determine whether any of these names could apply to the early Miocene fossils. All but *Peronaeus* Albers, 1850, *Platybostryx* Pilsbry, 1896, *Phenacotaxus* Dall, 1912, *Scansicohlea* Pilsbry, 1930, and *Pampasinus* Weyrauch, 1958 can be dismissed for having embryonic whorls that are entirely smooth or having a combination of spiral and axial sculpture (the type of *Bostryx* sensu stricto, *B. solutus* (Troschel, 1847) has smooth embryonic whorls). *Elatibostryx* and *Kionoptyx* are disregarded because of their dissimilar embryonic whorl sculpture and/or shell morphology mentioned in the original descriptions (Haas, 1966: 239; Weyrauch, 1958: 113). *Peronaeus*, *Pampasinus*, and *Platybostryx* can be eliminated on the basis of shell shape. The first is greatly elongated, and the other two genera are thick and lens-shaped. *Phenacotaxus*, *Scansicohlea*, and *Tocobaga* have similar shell shapes, but do not agree in any other of the charaeters we use to distinguish the latter. *Phenacotaxus* and *Scansicohlea* have simple peristomes, their body whorls do not ascend near the aperture and are evenly expanded, not flattened behind the

Table 1. Shell morphometrics of type specimens of nominate forms of *Tocobaga*. L = shell length, W = shell width, ApL = aperture length, ApW = aperture width; all measurements in mm, X = no measurement possible. Bold species are considered valid.

vouchers	taxon	L	W	L/W	ApL	ApW	ApL/ ApW	no. of whorls	Complete
WFIS 865	***americanus***	15.9	8.4	1.9	8.2	4.9	1.7	6+	Yes
USNM 111971	*laxus*	15.1	8.1	1.9	7.2	4.8	1.5	6.5±	Yes
USNM 111970	*partulinus*	15.1	8.0	1.9	8.0	5.0	1.6	6±	No
ANSP 30607	***floridanus***	9.4	4.0	2.4	4.6	2.8	1.6	4±	No
USNM 165013	*ballistae*	8.6	4.2	2.1	3.2	2.0	1.6	5±	No
USNM 111962	*heilprinianus*	10.2	4.7	2.2	3.4	2.2	1.6	6±	No
USNM 165014	*remolina*	9.5	4.3	2.2	3.8	2.2	1.7	6±	No
USNM 111964	*stearnsii*	13.5	5.9	2.3	4.5	2.5	1.8	4±	No
USNM 165012	*tampae*	13.5	6.1	2.2	4.5	2.8	1.6	6.6	Yes
USNM 165015	*tortilla*	10.8	4.9	2.2	3.3	2.0	1.7	5±	No
USNM 495932	***wakullae***	26.5	X	X	14.1±	X	X	6±	No

peristome. It is clear that the morphology of *Tocobaga* is unique, that this taxon has no close resemblance to any of the name-bearing species currently synonomized with *Bostryx* sensu lato, and that consequently, none of these names can serve to accommodate the Florida fossils.

Examination of the holotypes of all named fossil "*Hyperaulax*" indicates that only three species are recognizable in the Florida fossils; the taxa described by Dall (1890, 1915) are synonyms of either *T. americanus* or *T. floridanus*. Below we diagnose and discuss each species. Shell length, shell width, aperture length, and aperture width (Tables 1–2) were measured as described in Crampton (1916) for similarly shaped *Partula*. We use the following institutional abbreviations: ANSP (Academy of Natural Sciences of Drexel University), UF (Florida Museum of Natural History, University of Florida), USNM (National Museum of Natural History, Smithsonian Institution), and WFIS (Wagner Free Institute of Science, Philadelphia).

Table 2. *Tocobaga americanus* (Heilprin, 1886) shell morphometrics; L = shell length, W = shell width, ApL = aperture length, ApW = aperture width; number of whorls of all measured fossils estimated at 6+ due to erosion of embryonic whorls. All measurements in mm.

Cat. No.	L	W	L/W	ApL	ApW	ApL/ApW
UF 66653a	15.6	7.7	2.03	7.1	4.8	1.48
UF 66653b	16.3	8.1	2.01	8.3	4.8	1.73
UF 66653c	14.5	7.5	1.93	7.8	4.5	1.73
UF 66653d	14.4	7.3	1.97	7.1	4.0	1.78
UF 66653e	16.3	7.5	2.17	7.8	4.9	1.59
UF 66653f	15.9	7.7	2.06	8.1	5.0	1.62
UF 66653g	15.5	8.0	1.94	8.3	4.8	1.73
UF 66653h	16.3	8.2	1.99	8.1	5.0	1.62
UF 66653i	15.7	7.9	1.99	7.9	4.3	1.84
UF 66653j	14.8	7.2	2.06	7.2	5.0	1.44
UF 66653k	14.4	7.9	1.82	7.8	4.9	1.59
UF 66653l	17.7	8.3	2.13	8.7	4.7	1.85
UF 66653m	15.8	8.3	1.90	8.4	4.8	1.75
UF 66653n	17.3	8.3	2.08	8.0	5.5	1.46
UF 66652	17.1	8.5	2.01	8.6	5.1	1.69
UF 66651	16.3	7.8	2.09	8.4	4.5	1.87
Mean	15.9	7.9	2.01	8.0	4.8	1.67
SD	1.01	0.39	0.09	0.50	0.35	0.14

SYSTEMATICS

Tocobaga americanus (Heilprin, 1886) new combination

(Figures 3–7, Tables 1 and 2)

Partula americana Heilprin, 1886: 115, pl. 16, fig. 60.

Bulimulus (? *Anctus*) *americanus* var. *partulinus* Dall, 1890: 7; 1915: 26, pl. 4, fig. 12.

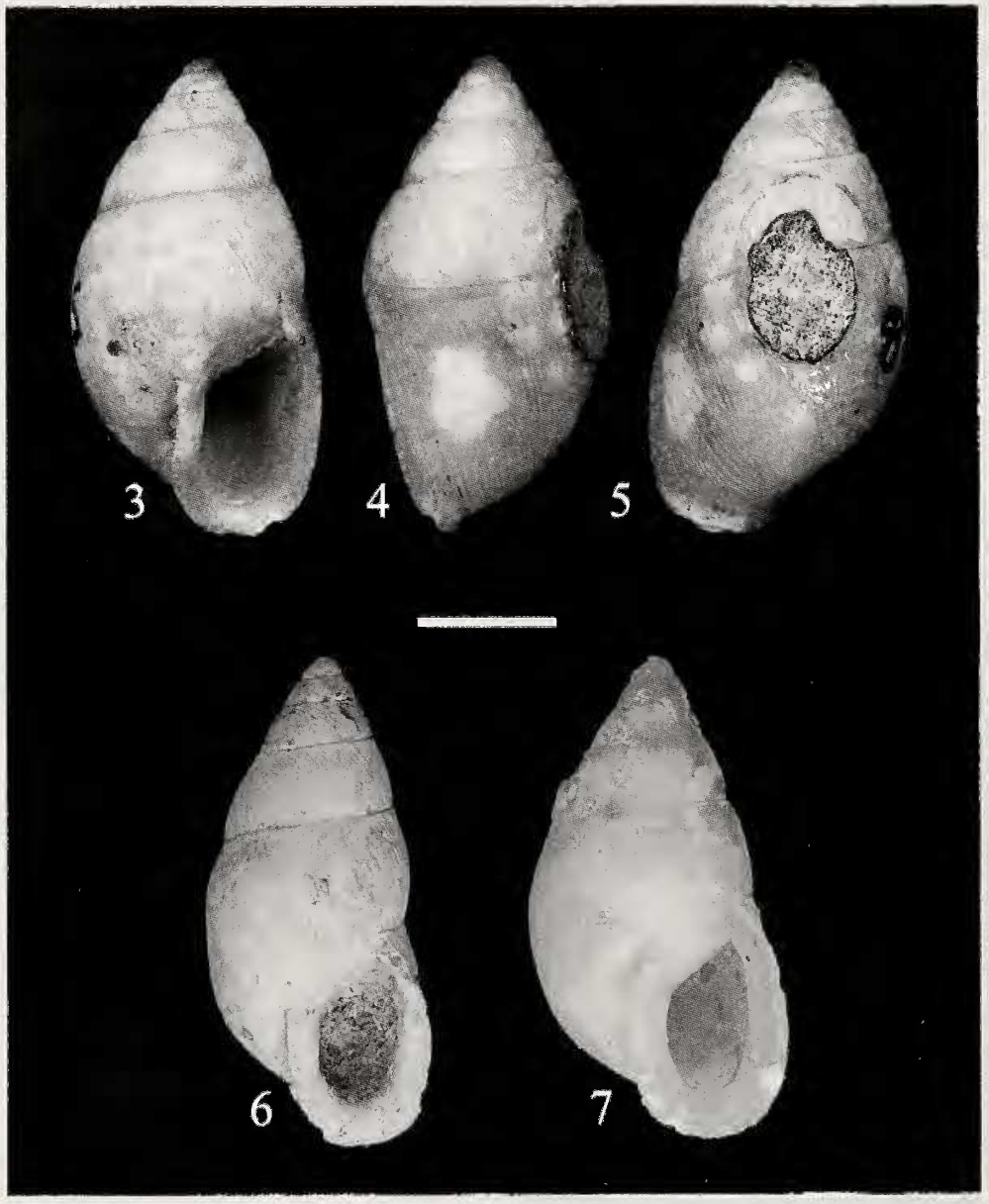
Bulimulus (? *Anctus*) *americanus* var. *laxus* Dall, 1890: 7; 1915: 26, pl. 4, fig. 14.

Bulimulus (*Hyperaulax*) *patulinus* Mansfield, 1937: 24–25 (*lapsus calami*)

Diagnosis: A large species of *Tocobaga*, 15–17 mm in height, 6–8 mm in width; shell ovate in shape; whorls approximately 5.5–6.5, slightly convex; shell sculpture of evenly spaced oblique riblets of width equal to their interspaces; last half of body whorl slightly flattened, ascending for last 0.2 whorl; aperture subquadrate; peristome with a wide, flat expansion, thickened internally throughout, almost complete, inner and outer margins connected by a thickened parietal callus; a narrow channel present at posterior insertion of outer lip, parallel to the long shell axis; umbilicus narrow; columella simple and straight.

Holotype: WFIS 865 (Figures 3–5) Ballast Point, Hillsboro [Hillsborough] Bay, [Tampa, Hillsborough County], Florida, upper Tampa Member, Arcadia Formation (early Miocene). J. Willcox and A. Heilprin, 1886.

Remarks: *Tocobaga americanus* is readily distinguished from *T. floridanus* by its larger size and more ovate shape; more rapidly expanding whorls; peristome that is expanded along the entire outer margin; channel at



Figures 3–7. *Tocobaga americanus* (Heilprin, 1886). **3–5.** Holotype of *Partula americana* Heilprin, 1886. WFIS 865. **6.** Holotype of *Bulimulus americanus* var. *laxus* Dall, 1890. USNM 111971. **7.** Holotype of *Bulimulus americanus* var. *partulinus* Dall, 1890. USNM 119970. Scale bar = 5 mm.

the posterior insertion of the outer lip that is parallel to the main axis of the shell; and a more open umbilicus.

The holotypes of Dall's (1890) varieties *laxus* (Figure 6) and *partulinus* (Figure 7) are indistinguishable from typical *T. americanus* in any important detail. The shells of *laxus* are more slender and have stronger axial sculpture, while those of *partulinus* are even more slender. However, both are also shorter in length than typical *T. americanus* and all three have identical length to width ratios. Similarly, the length to width ratios of the aperture is also alike (Table 1). Variation among 16 unbroken individuals of 59 specimens in UF lots 66651, 66652, and 66653 (Table 2) include a morphological range in shell length and width and apertural length and width that encompasses the two varietal names and we see no need to recognize this natural variation with formal epithets. Specimens from Wakulla County, Florida questionably referred to these forms (Mansfield, 1937) were not located.

Material Examined: *Partula americana* Heilprin, 1886, Holotype, WFIS 865; *Tocobaga americanus* (Heilprin, 1886), UF 66651 (1), UF 66653 (57), USNM 111965 (1); *Bulimulus americanus* var. *partulinus* Dall, 1890, Holotype, USNM 111970; *Bulimulus americanus* var. *laxus* Dall, 1890, Holotype, USNM 111971.

***Tocobaga floridanus* (Conrad, 1846) new combination**
(Figures 8–16, Table 1)

Bulimus floridanus Conrad, 1846: 399, text-figure.
Bulimus (*Bulimulus*) *longaevus* Ancey, 1881: 414.
Bulimulus (? *Anctus*) *heilprinianus* Dall, 1890: 6–7, pl. 1, figs. 6b, 10.
Bulimulus (? *Anctus*) *stearnsii* Dall, 1890: 7–8, pl. 1, fig. 12.
Bulimulus (*Hyperaulax*) *ballistae* Dall, 1915: 26–27, pl. 1, fig. 5.
Bulimulus (*Hyperaulax*) *remolina* Dall, 1915: 27–28, pl. 1, fig. 18.
Bulimulus (*Hyperaulax*) *tampae* Dall, 1915: 26, pl. 1, fig. 3.
Bulimulus (*Hyperaulax*) *tortilla* Dall, 1915: 27, pl. 1, fig. 2.

Diagnosis: A smaller species of *Tocobaga*, 8.1–14.1 mm in height, 3.6–6.0 mm in width; shell ovate to ovate cylindrical in shape; whorls 5–6.5, slightly convex to flattened; embryonic whorl blunt, rounded, sculpture unknown; shell sculpture of evenly spaced oblique riblets of width equal to their interspaces, weak spiral incised lines occasionally present in interspaces; body whorl not evenly expanded, last half whorl slightly flattened, ascending last 0.2 whorl; aperture oval to subquadrate; peristome expanded, thickened on inner margin along the columellar area, basally and along anterior half of outer lip; inner and outer peristome connected by a parietal callus; narrow channel present at posterior insertion of outer lip that is deflected medially at 45° relative to shell long axis; umbilicus very narrow, chink-like; columella simple and straight.

Holotype: ANSP 30607 (Figures 8–10). Nine miles from Tampa on Hillsboro [Hillsborough] River, [Hillsborough County], Florida, upper Tampa Member, Arcadia Formation (early Miocene). The holotype is a broken specimen. The inadequate original text-figure apparently depicts a reconstruction.

Remarks: *Bulimulus longaevus* Ancey, 1881 is an unnecessary replacement name for *Bulimus floridanus* Conrad, 1846 (see Henderson, 1935), not *B. floridanus* Pfeiffer,

Figures 8–16. *Tocobaga floridanus* (Conrad, 1846). **8–10.** Holotype of *Bulimus floridanus* Conrad, 1846. ANSP 30607. **11.** Holotype of *Bulimulus ballistae* Dall, 1915. USNM 165013. **12.** Holotype of *Bulimulus heilprinianus* Dall, 1890. USNM 111962. **13.** Holotype of *Bulimulus remolina* Dall, 1915. USNM 165014. **14.** Holotype of *Bulimulus stearnsii* Dall, 1890. USNM 111964. **15.** Holotype of *Bulimulus tampae* Dall, 1915. USNM 165012. **16.** Holotype of *Bulimulus tortilla* Dall, 1915. USNM 165015. Scale bar = 5 mm.

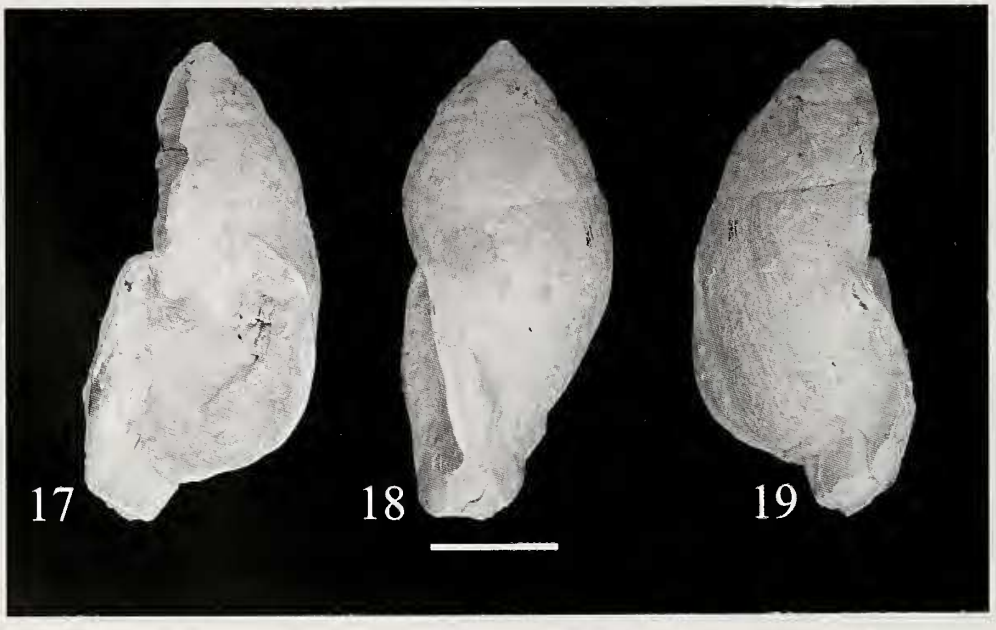
1857, as demonstrated by Wood and Gallichan (2008: 60). Ancey (1881: 414) erroneously stated that *B. floridanus* Pfeiffer, 1857 was described prior to Conrad's taxon (1846), leading Wood and Gallichan (2008) to misinterpret Ancey's intent. The holotypes of Dall's species *Bulimulus ballistae*, *B. heilprinianus*, *B. remolina*, *B. stearnsii*, *B. tampae*, and *B. tortilla* while differing in size are all similar in shape (Figures 8–16) and shell length to width and aperture length to width ratios both to each other and to the holotype of *Bulimus floridanus* (Table 1). The holotype of *Bulimulus ballistae* (Figure 11) is nothing more than a rather small specimen of *Tocobaga floridanus* differing from that species in no obvious detail. The holotypes of *Bulimulus heilprinianus* (Figure 12) and *Bulimulus tortilla* (Figure 16) differ from the typical *T. floridanus* only in having a more pronounced thickening on the anterior half of the inner margin of the outer lip. The holotype of *B. floridanus* is not fully mature and so does not prominently exhibit this character. The holotype of *Bulimulus tampae* (Figure 15) is merely a large specimen of *T. floridanus* and differs in no characters other than its size. The holotype of *Bulimulus remolina* (Figure 13) is slightly more elongate than typical *T. floridanus* and has a rather flattened body whorl with the sculpture largely eroded. The holotype of *Bulimulus stearnsii* (Figure 14) is the most unusual specimen examined. This specimen is quite elongate and large; with narrow, flattened whorls; almost lacking in shell sculpture. We believe the smooth surface is due to erosion, because traces of the characteristic ribbing of *Tocobaga* remain on a few surfaces, most prominently behind the aperture. The specimen's large size and elongate shape appear to represent one extreme of the variation in *T. floridanus*. The holotype of *B. remolina* and other specimens (USNM 646161) are intermediate in shape between the holotype of *B. floridanus* and that of *B. stearnsii*, or are equally as flattened as the type of *B. stearnsii*, although not as large. The extreme elongation in the holotype of *B. stearnsii* is partly, but not entirely, a reflection of its large size, though other large specimens of *T. floridanus* (e.g., USNM 646160) are more ovate in shape. Given the continuum in size and shape that occurs between the holotypes of *B. floridanus* and *B. stearnsii*, and the apparently eroded nature of the latter's smooth surface, we believe the holotype of *B. stearnsii* represents one extreme of the morphological variation seen within *T. floridanus*.

Material Examined: *Bulimus floridanus* Conrad, 1846, holotype, ANSP 30607; *Tocobaga floridanus* (Conrad, 1846), USNM 111960 (1), USNM 111961 (7) USNM 646160 (5), USNM 646161 (5), USNM 646162 (1); *Bulimulus heilprinianus* Dall, 1890, holotype, USNM 111962; *Bulimulus stearnsii* Dall, 1890, holotype, USNM 111964; *Bulimulus tampae* Dall, 1915, USNM 165012; *Bulimulus ballistae* Dall, 1915, holotype, USNM 165013; *Bulimulus remolina* Dall, 1915, holotype, USNM 165014; *Bulimulus tortilla* Dall, 1915, holotype, USNM 165015.

***Tocobaga wakullae* (Mansfield, 1937) new combination**
(Figures 17–19, Table 1)

Bulimulus americanus wakullae Mansfield, 1937: 15:70, pl. 1, figs. 10, 13.

Diagnosis: A large species of *Tocobaga*, ca. 26 mm in height, >10 mm in width; shell ovate in shape; whorls approximately 6.5, slightly convex; embryonic whorl blunt, rounded, sculpture unknown; later whorl sculpture of



Figures 17–19. *Tocobaga wakullae* (Mansfield, 1937). Holotype of *Bulimulus americanus wakullae* Mansfield, 1937. USNM 495932. Scale bar = 5 mm.

evenly spaced axial riblets more or less parallel to shell long axis, spiral sculpture not apparent; body whorl very slightly flattened behind apertural lip, ascending very slightly for last 0.2 whorl; aperture ovate, slightly oblique; peristome moderately reflected, but not greatly expanded or thickened within; parietal area with weak callus; channel at posterior insertion of outer lip not apparent; characters of umbilical area unknown; columella simple, unadorned.

Holotype: USNM 495932 (Figures 17–19). About 200 yards south of Wakulla Railroad Station, Wakulla County, Florida. External mold and cast.

Remarks: Mansfield (1937) originally placed this taxon as a subspecies of *Tocobaga americanus*, but it differs from that species in its larger shell size, in having an ovate instead of subquadrate aperture, in its more inflated shape, and in having the axial shell sculpture oriented more nearly parallel to the long axis of the shell. These differences in shell characters lead us to conclude that these two taxa are separate species.

Our assignment of this taxon in *Tocobaga*, however, is not without reservation. Several of the diagnostic features of that genus, such as the embryonic whorl sculpture, the channel at the posterior insertion of the outer lip, and the nearly complete peristome, cannot be examined in the holotype of *B. wakullae* (the only specimen available to us) because of its poor preservation (an external mold) and casting material. Collection of additional material may allow assessment of these particular characters, whereby the generic allocation of *B. wakullae* may well be revised.

Tocobaga wakullae (Mansfield, 1937) was described from the "Tampa Limestone" of Wakulla County in northwestern Florida. Although Mansfield (1937) did not discuss the stratigraphy of the type locality, the type specimen was probably collected from what is now considered the St. Marks Formation. This formation is early Miocene in age (Rupert and Spencer, 1988) and approximately contemporaneous with the upper Tampa Member (Arcadia Formation) of the Tampa Bay area.

Material Examined: *Bulimulus americanus wakullae* Mansfield, 1937, Holotype, USNM 495932, external mold and cast.

BIOGEOGRAPHY

Modern orthalicoids are particularly diverse in South America with a few lineages in Africa, Australia, Melanesia, and New Zealand. The group appears to have a Gondwanan distribution (Herbert and Mitchell, 2009). However, the family is well represented in Mexico, Central America, and the Antilles and there are representatives of a few genera in temperate North America including the bulimulids *Drymaeus* and *Rabdotus*. Several other Antillean land snail groups were widely distributed in North America during the late Cretaceous and early Tertiary (Bishop, 1979; Roth and Hartmann, 1998) and became restricted to the Antilles as climate cooled in the Tertiary. However, the oldest North American fossil bulimulids are the Florida Miocene fossils reviewed here and there is yet no evidence that bulimulids were present in North America before then. The oldest bulimulids are from a middle Paleocene site in southern Brazil where the family accounts for more than 30% of fossil species diversity (Salvador and Simone, 2013). The family remains the most diverse family in South America accounting for approximately 45% of recent South American species (Simone, 2006).

Many of the Florida Tampa Member (Arcadia Formation) land snails are similar in shell morphology to extant Antillean species (Pilsbry, 1897a; Auffenberg and Portell, 1990). Fossil species were assigned to the extant Antillean genera *Plagioptycha* Pfeiffer, 1855, *Cepolis* de Montfort, 1810, and *Pleurodonte* Fischer de Waldheim, 1807, *Gongylostoma* Albers, 1850, and *Cerion* Röding, 1798 (Dall, 1915; Mansfield, 1837). While the placement of these fossil taxa in modern genera can be questioned, the fauna surely has a degree of Caribbean affinity. The Antillean component of the Tampa Member (24–22.5 Ma, but see Scott, 1988) species apparently dispersed over water to Florida after contact between the Caribbean Plate and the Bahama Platform 38 Ma (Duncan and Hargraves, 1984). Reexamination of the entire fauna may provide a better understanding of its biogeography.

Relationships between *Tocobaga* and recent bulimulid genera remain unknown. Fossiliferous deposits in North America have not yielded taxa closely similar to *Tocobaga* and the extinct South American fossil genera, *Paleobulimulus* Parodiz, 1949 and *Itaborahia* Maury, 1935, have shell morphologies quite unlike *Tocobaga* (Parodiz, 1969).

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